Effect of root zone temperature on ectomycorrhiza and vesicular–arbuscular mycorrhiza formation in disturbed and undisturbed forest soils of southwest Oregon

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Received December 13, 1982[1]
Accepted March 25, 1983

PARKE, J. L., R. G. LINDERMAN, and J. M. TRAPPE. 1983. Effect of root zone temperature on ectomycorrhiza and vesicular–arbuscular mycorrhiza formation in disturbed and undisturbed forest soils of southwest Oregon. Can. J. For. Res. **13**: 657–665.

The presence of ectomycorrhizal and vesicular–arbuscular (VA) mycorrhizal fungi in soils from five sites in a mixed conifer zone in southwest Oregon, each consisting of a 1- to 1.5-year-old clear-cut adjacent to an undisturbed forest stand, was determined by bioassay with *Pseudotsuga menziesii* (Mirb.) Franco, *Pinus ponderosa* Dougl. ex P. Laws & C. Laws, and *Trifolium subterraneum* L. 'Mt. Barker' as hosts grown at root zone temperatures ranging from 7.5 to 35°C. Maximum formation of both ectomycorrhizae and VA mycorrhizae occurred at 18.5–24°C in soils from all sites, and there were no significant qualitative or quantitative differences between disturbed (clear-cut) or undisturbed (forest) soils. Mycorrhiza formation was moderate even at the lowest temperature tested (7.5°C) but was greatly reduced or prevented at or above 29.5°C. Treatment of soil at 35°C for 1 week did not appear to adversely affect viability of ectomycorrhizal fungus propagules, but young mycorrhizae subjected to the same treatment appeared to be severely injured. Thus the ability of native mycorrhizal fungi to grow at low soil temperatures is especially important as they may contribute to the survival of seedlings outplanted into climatic zones characterized by warm, dry summers following cool, wet winters and springs.

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En se servant de *Pseudotsuga menziesii* (Mirb.) Franco, de *Pinus ponderosa* Dougl. ex P. Laws & C. Laws et de *Trifolium subterraneum* L. 'Mt. Barker' comme hôtes vivants croissant à des températures de 7,5 à 35°C au niveau des racines, les auteurs ont déterminé la présence de champignons ectomycorhiziens et endomycorhiziens à vésicules et arbuscules (VA) dans les sols de cinq stations d'une forêt mixte de conifères, au sud-ouest de l'Orégon, chaque station étant constituée d'une zone coupée à blanc il y a 1 à 1,5 an, adjacente à un peuplement non perturbé. La formation maximale de mycorhizes des deux types s'est produite dans l'intervalle 18,5–24°C, dans les sols de toutes les stations, sans montrer de différences qualitative et quantitative significatives entre les sols de la zone perturbée (coupe à blanc) et la forêt non perturbée. La température la plus basse expérimentée (7,5°C) a permis une formation modérée de mycorhizes mais à 29,5°C et plus, cette formation a grandement été réduite ou annihilée. La viabilité des éléments de propagation des champignons ectomycorhiziens n'a pas semblé être affectée lorsque le sol fut traité à 35°C pendant 1 semaine, traitement qui cependant a causé des dommages poussés aux jeunes mycorhizes. La capacité des champignons indigènes mycorhiziens de se développer à de basses températures du sol est donc particulièrement importante; ils peuvent contribuer à la survie des semis transplantés dans des zones climatiques aux étés chauds et secs suivis d'hivers et de printemps frais et humides.

[Traduit par le journal]

Introduction

Earlier studies of sites in southwest Oregon and northern California indicated that the inoculum potential of ectomycorrhizal fungi in soil may be lower in old clear-cuts (average age = 9.4 year) than in adjacent forest stands (Parke *et al.* 1983*b*). Many soil properties may be altered during a long time period following and as a result of clear-cutting and burning, including changes in soil physical properties, vegetation, nutrient availability, soil temperature, organic matter, and associated soil microorganisms. It was not clear from that study if disturbance *per se* or the concomitant changes produced by disturbance were responsible for the apparent reduction in ectomycorrhizal inoculum potential.

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[1] Revised manuscript received March 15, 1983.

Temperature is known to influence development of ectomycorrhizae, although differences in response occur among species and isolates, suggesting adaptation to climate (Marx *et al.* 1970; Marx and Bryan 1971; Theodorou and Bowen 1971; Marais and Kotzé 1978; Dixon *et al.* 1981). Seasonal fluctuations in the abundance of ectomycorrhizae have also been observed in nursery and forest soils and are at least partially attributable to temperature effects (Sinclair 1974; Harvey *et al.* 1978; Vogt *et al.* 1980). The effect of soil temperature on the growth of ectomycorrhizal fungi native to forest soils in southwest Oregon is not known.

The climate in southwest Oregon is characterized by cool wet winters and warm dry summers, with most of the 820-mm average annual precipitation occurring as rain during October–March (Sterns 1960; Waring and Franklin 1979). Mean monthly temperature ranges from 4°C (January) to 20°C (July). Conifer root growth begins in early spring when temperatures reach about 5.5°C. Root growth activity peaks in the weeks preceding bud burst in midspring and is reduced to a low level until fall rains initiate a second, smaller peak of activity (Heiner and Lavender 1972; Cleary *et al.* 1978). Under controlled conditions when moisture is not limiting, root growth of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) from a southwest Oregon seed source is optimal at approximately 20°C (Lavender and Overton 1972). Twenty-four hour temperature data recorded 20 cm below the soil surface in clear-cuts during July ranged from predawn minima of 13°C to maxima of 31°C (6:30–10:30 p.m.) (S. D. Hobbs, personal communication).

Clear-cut areas are naturally invaded by plant species which are characteristically vesicular–arbuscular (VA) mycorrhizal (J. L. Parke, unpublished observations). Since temperature is known to affect VA mycorrhizal fungus spore germination (Schenck *et al.* 1975), sporulation (Schenck and Smith 1982), growth, and root colonization (Furlan and Fortin 1973; Hayman 1974; Schenck and Schroder 1974; Smith and Bowen 1979; Schenck and Smith 1982), temperature effects on VA mycorrhizal fungi native to southwest Oregon forest soils were also investigated.

Objectives of our study were (*i*) to compare the temperature range and optima for root colonization by ectomycorrhizal and VA mycorrhizal fungi native to southwest Oregon, (*ii*) to compare the mycorrhizal colonization of roots grown in disturbed versus undisturbed soils, (*iii*) to determine if mycorrhizal fungi from disturbed versus undisturbed soils respond differently to temperature, (*iv*) to test survival of ectomycorrhizal propagules at sustained high temperature, and (*v*) to test the effects of high soil temperature on established ectomycorrhizae.

Materials and methods

Experiment 1

Five sites, each a 1- to 1.5-year-old clear-cut adjacent to an undisturbed forest stand, were chosen in the Roseburg area (Douglas County) of southwest Oregon. Located in the Coast Range north of the Siskiyou Mountains, this area is characterized as a mixed-conifer zone (Franklin and Dyrness 1973) with Douglas-fir the prevalent tree species. All clear-cuts had been burned. Mean soil pH was 6.1 with 14 μg/g Olsen available phosphorus, 7.5 μg/g ammonium nitrogen, 11.1 μg/g nitrate nitrogen, and 6.9% organic matter. The sparse vegetation in the clear-cuts consisted mainly of grasses, herbs, and hardwoods sprouted from stumps. Each site is briefly identified below and vegetation of the undisturbed portion of each site described.

1. *Iverson* (T28S R8W S15): Elevation 427 m, E aspect, 30% slope. Kanid gravelly loam. *P. menziesii*, *Calocedrus decurrens* (Torr.) Florin, *Pinus ponderosa* Dougl. ex P. Laws & C. Laws, *Arbutus menziesii* Pursh, *Taxus brevifolia* Nutt., *Abies grandis* (Dougl.) Forbes, *Gaultheria shallon* Pursh, *Vaccinium membranaceum* Dougl., *Polystichum munitum* (Kauf.) Presl., *Pteridium aquilinum* (L.) Kuhn.

2. *Tom Taylor* (T29S R8W S33): Elevation 488 m, W aspect, 10% slope. Jory silty clay loam. *P. menziesii*, *C. decurrens*, *P. ponderosa*, *A. menziesii*, *A. grandis*, *Berberis nervosa* Pursh, *V. membranaceum*, *G. shallon*, *Arctostaphylos* sp.

3. *Days Creek* (T29S R5W S31): Elevation 365 m, W aspect, 20% slope. Jory silty clay loam. *P. menziesii*, *P. ponderosa*, *Pinus lambertiana* Dougl., *C. decurrens*, *A. grandis*, *G. shallon*, *B. nervosa*

4. *South Fork Middle Creek* (T31S R6W S35): Elevation 853 m, SE aspect, 70% slope. McGinnis very gravelly loam. *P. menziesii*, *P. lambertiana*, *C. decurrens*, *A. menziesii*, *Castanopsis chrysophylla* (Dougl.) DC., *Xerophyllum tenax* (Pursh) Nutt., *Ribes* spp., *G. shallon*, *B. nervosa*

5. *Boomer Hill* (T29S R6W S33): Elevation 610 m, N aspect, 35% slope. Beekman very gravelly loam. *P. menziesii*, *C. decurrens*, *A. menziesii*, *A. grandis*, *G. shallon*, *Polystichum* sp.

Soil was collected in January just prior to planting of conifer seedlings on the clear-cuts. One-litre soil samples were collected from the top 0–10 cm of mineral soil at 5-m intervals along three 20-m transects (15 samples total in each disturbed and each undisturbed area) for each of the five sites. Soil was sieved through 5-mm mesh to remove stones and large woody debris but permit passage of root fragments. The 15 samples from each area were then combined, mixed (1:1) with coarse vermiculite and sown with surface-sterilized Douglas-fir, ponderosa pine, or subterranean clover (*Trifolium subterraneum* L. 'Mt. Barker') seeds in 50-cm^3 tubes

(Ray Leach "Cone-tainer" Nursery, Canby, Oregon[2]). Final pH of the soil mixtures ranged from 4.9 to 6.6. Each soil had 15 replications per temperature treatment for each plant host. Clover plants were inoculated with *Rhizobium*. Controls consisted of pasteurized (65°C for 30 min aerated steam) soil blends. When plants emerged, the replicates of each host–soil combination were randomly placed in controlled temperature "air bath" boxes which maintained root zone temperature at 7.5, 13, 18.5, 24, 29.5, or 35 ± 0.5°C for the remainder of the experiment. Temperatures were monitored every 15 min with a 12-point thermograph recorder. Plant shoots were exposed to ambient greenhouse temperatures (24°C day : 18°C night) with a 16-h photoperiod (240 μE m^{-2} s^{-1}). Beginning 6 weeks after germination, plants were fertilized weekly with 3 mL Long-Ashton solution (Hewitt 1966) at one-quarter strength phosphorus. Plants were harvested 14 weeks (Douglas-fir, ponderosa pine) or 10 weeks (clover) after germination. Conifer roots were washed and examined for ectomycorrhizal fungus colonization. Total number of root tips, number and percent of root tips which were mycorrhizal, total root length (using a map measurer), shoot height, shoot dry weight, and root dry weight were recorded for each seedling. Mycorrhizal tips were classified according to morphological type. Clover roots were cleared and stained by a modification of the Phillips and Hayman (1970) technique and percent root length colonized by VA fungi assessed (Biermann and Linderman 1981). Dry weight of clover shoots was also recorded.

Experiment 2

Soil from site 2 (Tom Taylor) was mixed 1:1 with coarse vermiculite and incubated at 35°C for 0, 4, 12, 24, 72 h and for 1 week prior to sowing with Douglas-fir seeds. At this time, tubes were placed in an 18.5°C temperature box to maximize ectomycorrhiza formation. Seedlings were harvested 14 weeks after germination and assessed for mycorrhizae and plant parameters as described for experiment 1.

Experiment 3

Sixty tubes of the same soil mixture (experiment 2) were sown with Douglas-fir seeds and placed in an 18.5°C temperature box. Fourteen weeks following germination, 20 tubes were harvested and evaluated for mycorrhizae and plant growth. Twenty tubes were transferred to a 35°C temperature box, and 20 tubes remained in the 18.5°C box for an additional 4 weeks before both treatments were harvested and evaluated.

Results

Experiment 1

Optimal temperature for Douglas-fir mycorrhiza formation was 18.5°C for undisturbed forest soil and 24°C for clear-cut soil; 24°C was optimal for ponderosa pine mycorrhizae (Figs. 1 and 2). Colonization of both hosts was substantially reduced at 7.5, 13, 29.5, and 35°C. Clear-cut and undisturbed forest soil sources did not differ significantly at any temperature for either host. Sites did not differ significantly from each other in response to temperature, so the data have been combined. Percent of roots which were mycorrhizal, number of mycorrhizae per centimetre root, and number of mycorrhizae per seedling showed parallel trends; therefore, only percent mycorrhizae are reported. Composition of mycorrhizae by morphological type was influenced by temperature (Figs. 3 and 4). A white rhizomorphic type predominated at all temperatures for Douglas-fir and was favored at 18.5–24°C; this type

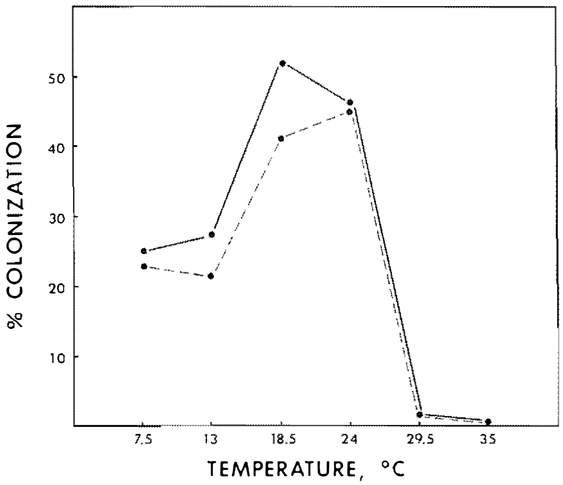

FIG. 1. Effect of root zone temperature on percent mycorrhizal colonization of Douglas-fir roots. —, undisturbed forest soil; – –, clear-cut soil.

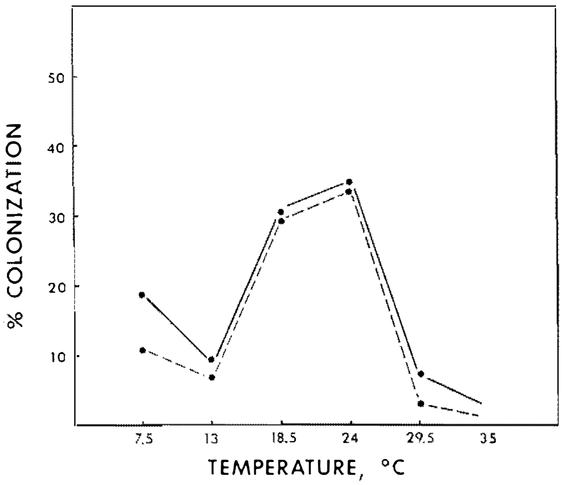

FIG. 2. Effect of root zone temperature on percent mycorrhizal colonization of ponderosa pine roots. —, undisturbed forest soil; – –, clear-cut soil.

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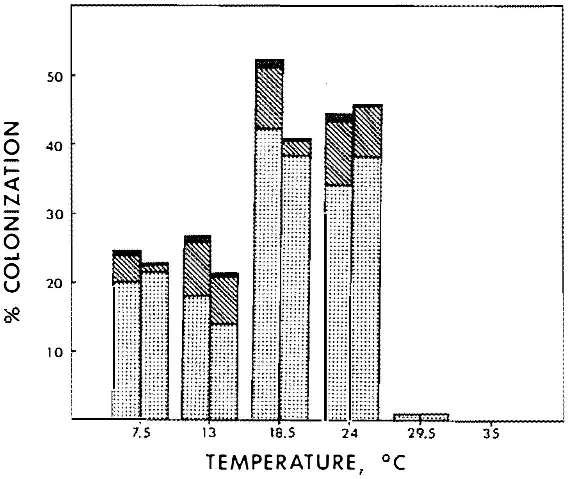

FIG. 3. Effect of temperature and disturbance on composition of Douglas-fir ectomycorrhizae by morphological type. ░, white rhizomorphic; ▨, brown; ■, *Cenococcum geophilum*. Left-hand column of each pair = undisturbed forest soil; right-hand column of each pair = clear-cut soil.

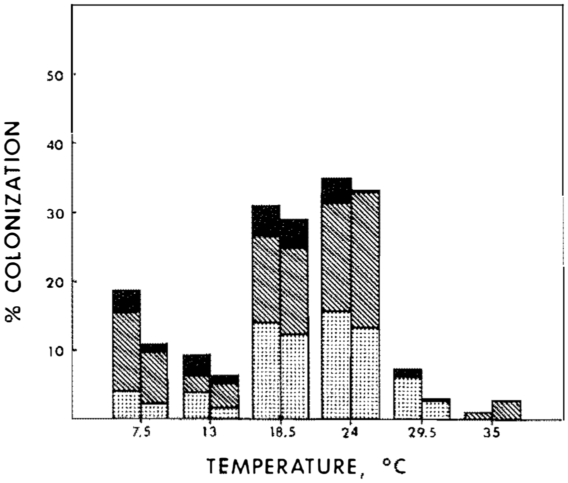

FIG. 4. Effect of temperature and disturbance on composition of ponderosa pine ectomycorrhizae by morphological type. ░, white rhizomorphic; ▨, brown; ■, *Cenococcum geophilum*. Left-hand column of each pair = undisturbed forest soil; right-hand column of each pair = clear-cut soil.

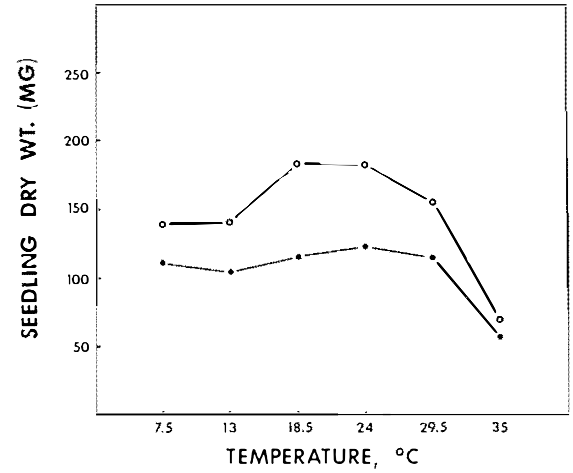

FIG. 5. Douglas-fir seedling dry weight as affected by root zone temperature. ●, clear-cut and undisturbed forest soils combined; ○, nonmycorrhizal controls.

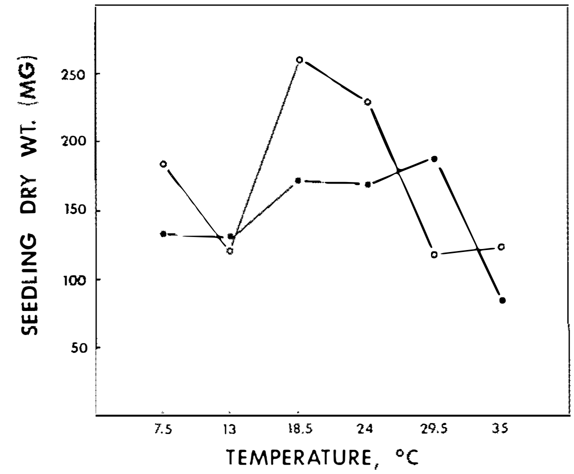

FIG. 6. Ponderosa pine seedling dry weight as affected by root zone temperature. ●, clear-cut and undisturbed forest soils combined; ○, nonmycorrhizal controls.

was predominant only at 18.5–29.5°C for ponderosa pine. A swollen brown type and to a lesser extent, *Cenococcum geophilum* Fr. mycorrhizae, were also found. Mycorrhizal plants were similar in size or smaller than nonmycorrhizal control plants except at 29.5°C for ponderosa pine (Figs. 5 and 6). Root and shoot growth of both hosts was largest at 18.5 or 24°C except for mycorrhizal ponderosa pine, for which the optimum was 29.5°C. A smaller percentage of ponderosa pine short roots were mycorrhizal than of Douglas-fir except at 29.5 and 35°C. Shoot/root ratios for all treatments showed similar trends with values near 1.0 occurring over the range 18.5–29°C (Fig. 7).

Optimal temperature for VA mycorrhizal development on clover was 18.5°C (65% of root length colonized) (Fig. 8). Colonization was reduced to 35% at 7.5°C and 10% at 29.5°C. No colonization occurred at 35°C. Infection levels did not differ significantly between clear-cut and undisturbed forest soils at any temperature. Optimal temperature for clover shoot growth was 24°C (Fig. 9). Mycorrhizal plants were significantly larger than nonmycorrhizal control plants at all but two temperatures (7.5, 18.5°) where differences in growth were not significant (Fig. 9). Although

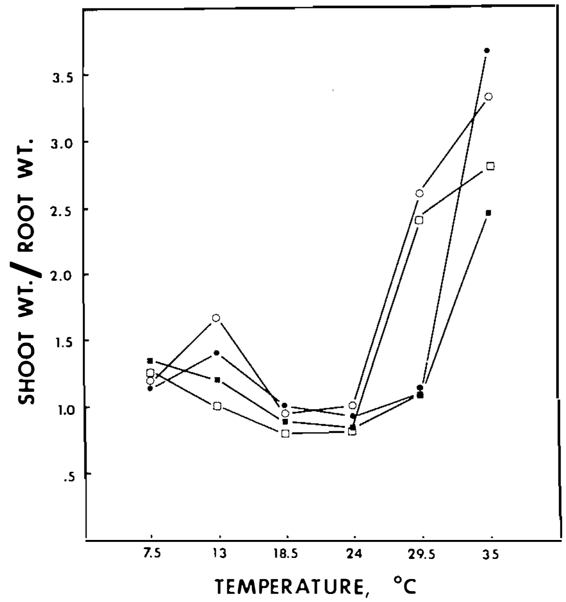

FIG. 7. Effect of root zone temperature on shoot weight/root weight of Douglas-fir (●) and ponderosa pine (■) seedlings; clear-cut and undisturbed forest soils combined (○), nonmycorrhizal controls (□).

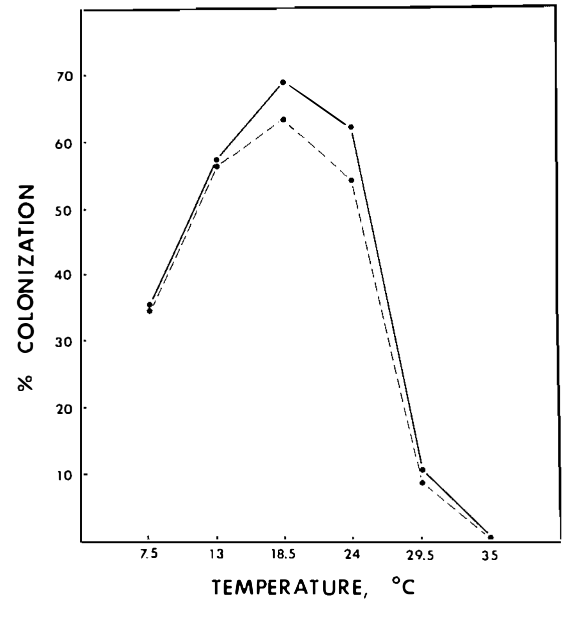

FIG. 8. Effect of root zone temperature on percent clover root length colonized by VA fungi. —, undisturbed forest soil; — —, clear-cut soil.

percent root colonization was not significantly different between mycorrhizal plants grown at 18.5 and 24°C, striking growth enhancement occurred at 24°C, possibly indicating a temperature effect on external hyphae.

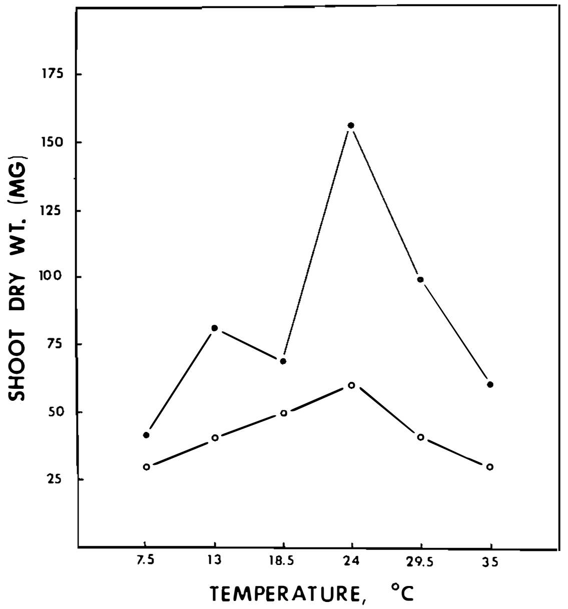

FIG. 9. Effect of root zone temperature on shoot dry weight of clover. ●, clear-cut and undisturbed forest soils combined; ○, nonmycorrhizal controls.

Colonization of clover roots was by a fine endophyte, *Glomus tenue* (Green.) Hall, in all treatments over the range of temperatures tested. Other endophytes were rarely present (<10%) and spores were not found.

Experiment 2

Percent mycorrhizae did not differ significantly ($P < 0.1$) in response to the various durations of soil pretreatments at 35°C. Plant growth was also unaffected by soil pretreatment.

Experiment 3

At 14 weeks, 42% of the root tips were mycorrhizal (Table 1). This increased to 51% in the seedlings which remained at 18.5°C and were harvested 4 weeks later. Only 21% of the root tips on seedlings transferred to 35°C were mycorrhizal. Root weight also declined for the seedlings transferred to the higher temperature. Mycorrhizae in the high temperature treatment appeared collapsed and moribund and lacked outgrowing hyphae and rhizomorphs. These mycorrhizae appeared physiologically inactive.

Discussion

In this study, temperature optima for both ectomycorrhiza and VA mycorrhiza development were lower than reported previously by many researchers (Marx and Bryan 1971; Marx *et al.* 1970; Theodorou and Bowen 1971; Furlan and Fortin 1973; Schenck and Schroder 1974; Schenck *et al.* 1975; Schenck and Smith 1982; Marais and Kotzé 1978; Smith and Bowen

TABLE 1. Effect of high temperature on established ectomycorrhizae

Temperature (°C)	Weeks	No. of mycorrhizae	% mycorrhizae	Shoot dry weight (mg)	Root dry weight (mg)
18.5	14	24.1*a* (4.1)	42.5*a* (5.8)	88*a* (6)	87*a* (6)
18.5	18	25.9*a* (4.0)	51.0*a* (6.4)	110*b* (7)	123*b* (7)
18.5	14				
35	4	8.6*b* (1.9)	21.0*b* (4.7)	100*ab* (5)	76*a* (6)

NOTE: Values are means of 17 seedlings and ± SE (mean). Values in columns not followed by same letters are significantly different, $P < 0.05$ (Duncan's multiple range comparison).

1979; Dixon *et al.* 1981). Formation of ectomycorrhizae by fungi native to southwest Oregon forest soils was optimal at 18.5°C (with Douglas-fir) or 24°C (with ponderosa pine) and severely restricted at 29.5°C, well below the 33–35°C temperatures found by others to be optimal for *Pisolithus tinctorius* mycorrhiza development (Marx *et al.* 1970; Marais and Kotzé 1978; Dixon *et al.* 1981), and below the maximum recorded for southwest Oregon clear-cut sites. In our study, mycorrhiza formation was moderate even at the lowest temperature tested (7.5°C). Soilborne propagules of native ectomycorrhizal fungi survived an extended period of high soil temperature (1 week at 35°C) without any reduction in viability, but established, actively growing mycorrhizae were intolerant of that high soil temperature. It is unlikely that soil temperatures under natural conditions become high enough to kill "dormant" mycorrhizal propagules, but newly established mycorrhizae on the shallow root systems of conifer seedlings may be vulnerable to high soil temperature during the first summer after planting. After this time, roots probably extend below the zone where high temperature could restrict mycorrhizal activity. In a study of a Coast Range (Oregon) Douglas-fir stand, mycorrhizae were found as deep as 30–50 cm (Fogel and Hunt 1979). A reservoir of other propagules (spores, hyphae, sclerotia) is likely to survive deep in the soil profile, and air- or mammal-borne (Maser *et al.* 1978) spores may be deposited on the soil surface once or twice annually.

More important than heat tolerance may be the ability of mycorrhizal fungi to grow at cool soil temperatures (Theodorou and Bowen 1971). Since conifer seedlings are planted during the winter and early spring, rapid colonization by mycorrhizal fungi could enhance plant growth and survival through increased water and nutrient uptake before the onset of environmental stress in summer. Mycorrhiza establishment and rhizomorph formation may be critical to the survival of newly planted seedlings subjected to moisture stress (Parke *et al.* 1983).

Temperature optima for mycorrhiza development seem to reflect adaptation to climate and coincide with temperature optima for active root growth. Studies with *P. tinctorius* in the southeast United States show maximal development at a high soil temperature. The Georgia climate is characterized by warm summers with frequent precipitation and mild winters. Oregon's summer drought limits root growth to cooler, wet periods of the year. Temperature response of conifer root growth has been shown to vary according to seed source (Lavender and Overton 1972). Just as provenance is an important consideration in selecting seed for particular environmental conditions, so too could ecotypes of ectomycorrhizal fungi adapted to growth at cool soil temperatures but tolerant of high soil temperatures be selected for nursery inoculations and subsequent outplanting on harsh sites (Trappe 1977).

Interestingly, the amount of mycorrhiza formation did not differ significantly between clear-cut and undisturbed forest soils. This contrasts with a previous study in which the ectomycorrhiza inoculum potential of disturbed sites was less than in adjacent forest stands (Parke *et al.* 1983*b*). However, in the present study, only recently disturbed areas, more representative of sites currently being replanted with conifers, were sampled as contrasted with our earlier study where many older clear-cuts were examined.

Temperature did influence the species composition of mycorrhizae as indicated by morphological type, but mycorrhizae occurring in soil from clear-cuts and undisturbed forest were affected similarly, i.e., there did not appear to be increased tolerance to high temperatures among mycorrhizal fungi from clear-cuts.

It is possible that differences in mycorrhiza composition between disturbed and undisturbed sites were obscured because of limitations in visually identifying and classifying ectomycorrhizae, especially at the early stages of infection. However, numerous isolations of fungi from mycorrhizae all yielded a single fungus from the predominant "white type." *Cenococcum geophilum* was the only ectomycorrhizal symbiont encountered which was identifiable. Fruiting bodies of several ectomycorrhizal fungus species were collected from the undisturbed stands, indicating that although inoculum of several fungi was probably present, our bioassay conditions could have selected for fewer mycorrhizal fungi than might naturally occur. However, our data indicate that temperature was not a selective factor in the assays.

The response of VA mycorrhizal fungi was similar to that of the ectomycorrhizal fungi; again, the temperature optima and range reported here are cooler than that reported by many researchers and seem to reflect adaptation to climate as proposed by Schenck *et al.* (1975). Temperature influenced the degree of mycorrhizal colonization, but VA mycorrhizal fungi in soils from clear-cuts and undisturbed forests were affected similarly.

Our results differ from other studies on VA mycorrhizal fungi in natural systems which suggest that propagule numbers in soil are reduced in disturbed areas (Moorman and Reeves 1979; Reeves *et al.* 1979; Powell 1980). Our results indicated that no such reduction had occurred, even though the logging disturbance had removed many VA mycorrhizal hosts from the sites. Furthermore, the relatively higher soil temperatures of the clear-cut sites compared with adjacent forested areas theoretically could have reduced the inoculum potential. In our study, the use of a single harvest at a single soil dilution may have obscured differences in number of propagules between clear-cut and undisturbed forest soils, but there still appears to be adequate VA mycorrhizal fungus inoculum in the clear-cut site as indicated by our bioassays and examination of roots of VA mycorrhiza hosts invading the clear-cuts. Interestingly, all the families of plants that invaded the clear-cuts examined were hosts for VA mycorrhizal fungi (J. L. Parke, unpublished observations).

We were surprised by the lack of diversity of VA mycorrhizal fungus species in both the clear-cut and undisturbed forest soils. *Glomus tenue* was by far the dominant VA endophyte encountered. We cannot attribute the lack of diversity to relative differences in the two site situations since they were similarly dominated by *G. tenue*. If temperature was among the selective pressures limiting the number of VA mycorrhizal fungus species in those sites, we presume it to be a general pressure of the geographical area, not site disturbance. *Glomus tenue* has a worldwide distribution, however, occurring in forests (Johnson 1977), grasslands and pastures (Crush 1973*a*, 1973*b*; Rabatin 1979; Molina *et al.* 1978), and an alpine community (Read and Haselwandter 1981). It appears to be an important pioneer (Johnson 1977) capable of symbiosis under quite low soil phosphorus conditions (Crush 1973*b*; Powell 1979) such as those that prevailed in this study. Growth of western red cedar (*Thuja plicata* Donn) seedlings was severely limited in these soils pasteurized to eliminate mycorrhizal fungus inoculum. Inoculation of the soil with *G. tenue* propagules abundant in litter (decomposing needles, etc.) from undisturbed mixed conifer stands restored normal growth (Parke *et al.* 1983*a*). The nature of the propagules of mycorrhizal fungi on the litter is still unknown, but we do know that in the forest soils examined in this study, spores were not found by sieving. These findings are consistent with other reports of low spore numbers but high inoculum potential (Mosse and Bowen 1968; Gerdemann and Trappe 1974; Read *et al.* 1976; Redhead 1977; Schenck and Kinloch 1980), and suggest that other forms of inoculum are involved. Colonized roots and hyphae were shown by others to be important forms of inoculum in communities of perennial plants (Mosse and Bowen 1968; Read *et al.* 1976; Johnson 1977), but we would have expected spores to be a better means of survival of VA mycorrhizal fungi in disturbed soils, especially where temperatures become elevated due to exposure to solar radiation. A logical conclusion from our study would be that nonspore propagules can survive brief periods of high (35°C) temperatures. We should not assume, however, that these fungi survive clear-cut soils only as dormant propagules since some recent reports suggest that VA fungi may be capable of limited saprophytic growth on moribund roots of hosts or nonhosts or on organic debris (Hirrel *et al.* 1978; Parke and Linderman 1980; Ocampo and Hayman 1981; Warner and Mosse 1982), which could have been quite prevalent in the clear-cuts.

Acknowledgements

Financial support for this study was provided by the following public agencies and private forest organizations cooperating in the California–Oregon Plantation Studies (COPS): Boise Cascade Corp., Champion International Co., Fruitgrowers Supply Co., International Paper Co., Medford Corp., Southern Pacific Land Co., Roseburg Lumber Co., Sun Studs Corp., and the United States Bureau of Land Management. We wish to thank Mr. John Chamard and Ms. Joyce Eberhardt for their excellent technical assistance. Technical Paper No. 6636 of the Agricultural Experiment Station, Oregon State University, in cooperation with the Agricultural Research Service, United States Department of Agriculture.

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